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Phenological Drivers and Consequences for Solitary Bees

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Abstract

Phenology, or the timing of biological events, is critical for the development, reproduction, and survival of organisms. One of the most common biological responses to climate change is a shift in phenology. Therefore, an understanding of the drivers underlying changes in phenology is essential in understanding how organisms will respond to a changing environment. This is especially pertinent for organisms that provide critical ecosystem services, such as pollinators. Bees are the most important pollinators in wild and agricultural ecosystems. Solitary nesting bees comprise 90% of total bee diversity, and 65% of total bee diversity nests below ground. Yet, the majority of bee research is focused on above-ground, social species such as the European Honeybee (*Apis mellifera*) and Bumblebees (*Bombus spp.*). To better understand how the majority of bees will respond to environmental changes, we need to investigate the drivers and consequences of solitary bee phenology is critical. This dissertation first examines the effect of various dimensions of phenology on solitary-nesting bee reproductive output, and then dives into the environmental correlates of ground-nesting bee phenology. In a subalpine ecosystem, I studied how the timing, duration, and synchrony of nesting activity impact reproductive success for two solitary, above-ground nesting bee species. I found that synchrony is an important predictor of reproductive success for these bees; more synchronous nesting activity increased reproductive success in both species. Additionally, for one species, longer nesting durations increased reproductive output, while the timing of nesting activity had no effect on reproductive success in either species. In this same subalpine ecosystem, I manipulated the soil environment as a proxy for climate change and monitored the emergence phenology of solitary, ground-nesting bees. Here, I found that both soil temperature and soil moisture are important factors in the timing of emergence, but the direction and magnitude of these effects was interactive and

varied between years. Finally, I asked a similar question in a coastal dune ecosystem. I manipulated the soil moisture content for solitary, ground-nesting bees and tracked emergence and survival. Because soil moisture and soil temperature are inversely related, my manipulations also altered the soil temperature for these bees. In contrast to the subalpine ground-nesting bees, the coastal dune bee emergence phenology was unresponsive to shifts in the soil environment. Furthermore, the survival of these bees was not affected by soil conditions. Altogether, the results of these studies highlight the complexity of how solitary bees are interacting with their environment. Specifically, I show that the synchrony of phenological activity should be considered when assessing reproductive consequences of phenology. Additionally, phenological responses to the soil environment are context dependent. The drivers of ground-nesting bee phenology depend on interannual variation in the environment and are dependent on the ecosystem at large. My results offer crucial insights into how solitary nesting bees interact with their environment and improve our understanding of how these pollinators will respond to a changing climate.

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Dedication

I dedicate this dissertation to Dr. Michael Mesler. Thank you for inspiring a curiosity for the natural world and making me believe that I have what it takes to pursue a doctorate. I wouldn't be here without your mentorship and encouragement.

PREVIEW

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Chapter 1

Phenological drivers of reproductive success: the effect of onset, duration, and synchrony of nesting activity in solitary bees

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Plain- Language Abstract

How successfully an organism reproduces depends on the timing of a biological event, like when a plant flowers, when a hibernating animal emerges, or when a bird migrates. However, there are different aspects to the timing of an event, for example, the start, duration or length, and synchrony (overlap in time with others in the population) of the event can all affect reproduction in different ways. The start of an event like migration can dictate the climate and resource landscape a bird experiences when it reaches its breeding grounds. The duration of a flowering event can determine how many pollinators visit. Finally, the synchrony of an individual emerging from hibernation can determine mating success. The start of an event is most often studied, but the duration and synchrony of the event are often overlooked. This study explores how the start, duration, and synchrony of individuals impacts reproduction. We focused on two solitary nesting-bees (bees that do not live in colonies) in the Colorado Rocky Mountains and tracked their nesting activity (start, duration, and synchrony) and the number of successful offspring they produced. While the start of nest date did not affect reproductive outcomes, the duration of nesting had varying effects on offspring numbers. When we analyzed the synchrony of nesting activity relative to others in the population, we found that bees that built nests when the majority of bees in the population were nesting had higher offspring success, probably because they were able to find mates more easily. This suggests that nesting synchrony plays an important role in bee reproduction. Our results highlight the importance of analyzing different aspects of timing on reproduction.

Technical Abstract

Phenological distributions are widely hypothesized to have important fitness consequences for organisms. However, the specific timing of a biological event, such as event onset, is only one dimension of a phenological distribution. Other important dimensions include the duration and synchrony of biological events, but their fitness consequences are less understood, especially in mobile organisms where it is challenging to track individuals. We therefore investigated the reproductive consequences of multiple dimensions of the phenological distribution of nesting activity for two solitary, cavity-nesting bee species (*Megachile relativa*, *M. pugnata*) in the Colorado Rocky Mountains. We focused on the effect of nesting activity onset, duration of nesting activity, and synchrony of nesting activity within the population. Our results indicate that without considering multiple dimensions of nesting phenology—onset, duration, and synchrony—important reproductive consequences can be overlooked. Of the three phenological dimensions we investigated here we found that synchrony was the only one to influence reproductive success for each of the two bee species we studied. We find that nest activity onset did not affect reproductive success. The duration of nesting activity had mixed effects on reproductive success: for one species, nests that took longer to build resulted in more offspring the following year, but for the other species, we observed no significant effect. While the causes of these fitness effects are unknown and warrant further investigation, our study highlights the importance of considering multiple dimensions of phenological distributions to better understand their effects on fitness.

Introduction

Phenology, or the timing of biological events, is a key factor in an organism's ecology and evolution, as it determines the environmental context for its survival, growth, and reproduction (Forrest and Miller-Rushing, 2010). Phenology is commonly defined as a distribution of the timing of a life-cycle event, such as budding or flowering in plants, and includes the onset, peak, and conclusion of a biological event (Rathcke and Lacey, 1985; CaraDonna et al., 2014). However, these components do not fully describe a phenological distribution (Rathcke and Lacey, 1985; Ollerton and Lack, 1998). How long the event occurs (duration) and the relative timing of an individual within the population compared to the rest of the population (synchrony) are two other dimensions of a phenological distribution that can affect organism performance (Augspurger, 1983; Li et al., 2016; Iler et al., 2021; Wong and Forrest, 2021). Therefore, considering multiple dimensions of phenological distributions is necessary to advance our understanding of the fitness consequences of phenological variation.

There is ample empirical and theoretical evidence that the timing of biological events for individuals can have reproductive consequences (Farzan and Yang, 2018; Slominski and Burkle, 2021; Eeraerts et al., 2022). Timing is often measured as event onset. Individuals with particularly early onset dates can experience a variety of reproductive costs or benefits, depending on the ecological context. For example, individuals with activity at the start of a population-level distribution may experience unfavorable weather conditions and resource scarcity that can hinder reproductive efforts (Inouye, 2008; Thomson, 2010; Augspurger, 2013; Slominski and Burkle, 2021); in other contexts, however, these early individuals may also benefit from reduced intraspecific competition and predation, increasing their reproductive success (Iwasa and Levin, 1995; Straka et al., 2014; Wong and Forrest, 2021).

As with the onset of a biological event, the duration of a biological event can have a variety of reproductive consequences. Evidence suggests that both plants and animals often experience fitness benefits from being active for longer time periods (Rathcke and Lacey, 1985; Bosch and Vicens, 2006; Li et al., 2016; Wong and Forrest, 2021). The link between longer durations and reproductive benefits is hypothesized to be attributed to increased time for reproductive activities (e.g., Wong and Forrest, 2021). Longer durations can also reduce the likelihood of phenological mismatch with resources and increase mating opportunities (Ison et al., 2014; Li et al., 2016; Waananen et al., 2018). Additionally, the onset and duration of events might not be independent from one another. The onset of reproductive activity can influence the duration of reproductive activity, with earlier onsets being linked to longer durations (Wong & Forrest, 2021), but longer durations do not always follow earlier onset and can occur independently (Dunne et al., 2003; Slominski and Burkle, 2021; Chen et al., 2023).

A third dimension of phenological distributions is the synchrony of a biological event for an individual within a population. Synchrony integrates the relative timing and duration among individuals and therefore might have different effects on reproductive success compared to one of these phenomena alone (Janzen, 1967; Augspurger, 1983). More synchronous individuals overlap more in time with one another compared to less synchronous individuals. Variation in reproductive synchrony is hypothesized to be a life-history strategy that maximizes reproductive success in plants, primarily due to increased mating opportunities and decreased predation (Augspurger, 1983; Ims, 1990a; Elzinga et al., 2007; Waananen et al., 2018). However, it is unclear if reproductive synchrony plays a similar role in reproductive success for other organisms, including insects, which are likely subject to evolutionary pressures associated with

mating and predation as well. Less is known about the importance of reproductive synchrony in animals because it is more difficult to measure synchrony in mobile organisms.

Here, we investigate how multiple dimensions of a phenological distribution (onset, duration, and synchrony) of nesting activity period influence reproductive success in two solitary, cavity-nesting bees in the Colorado Rocky Mountains. We focus on nesting activity because this is the reproductive period when nests are constructed and offspring are produced, representing an essential component of reproduction and fitness of these organisms. First, we explore interannual variation in the onset, duration, and synchrony of nesting activity across one population of each of the two bee species. Next, we ask: Does variation in any of these three phenological components of nesting activity affect reproductive success? The two species, *Megachile relativa* and *M. pugnata*, are abundant in our study system, active mid-season, and forage from similar floral resources, but *M. pugnata* is 25 % larger than *M. relativa* (Pardee et al., 2022). These abundant bees allow us to investigate the importance of variation in different dimensions of phenology.

Materials and Methods

Study Site

We investigated three years of solitary bee nesting activity and offspring emergence from 2012–2015 in a subalpine ecosystem in the Colorado Rocky Mountains. This ecosystem is characterized by high interannual variability in climate conditions and growing season length (Inouye et al., 2002; CaraDonna et al., 2014; Cordes et al., 2020; Ogilvie and CaraDonna, 2022). Our study sites are located near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA (30°57.5' N, 106°59.3' W, 2900 m a.s.l) in the East River Valley of the Elk Mountains. The subalpine ecosystem has a short growing season (3–5 months) and is covered in snow for the

remainder of the year. The study area hosts over 150 bee species, which are primarily native. The non-native honeybee, *Apis mellifera*, does not occur there (Gezon et al., 2015; CaraDonna et al., 2017; Pardee et al., 2022).

Study Species

We focused on two species of subalpine, solitary, cavity-nesting bees that are common in the region: *Megachile relativa* (Cresson) and *M. pugnata* (Say) (Megachilidae). Cavity-nesting bees are ideal for exploring the effects of various dimensions of phenological distributions on reproductive success because they experience brief foraging and nesting periods and readily construct nest cells in cavities in artificial structures (hereafter “nesting-blocks”) (Krombein, 1967; Frankie et al., 1998; Forrest and Chisholm, 2017). Nesting-blocks are typically constructed of wooden blocks with holes or ‘cavities’ drilled into them, in which bees will construct their nests. As such, metrics such as onset and end dates of nest construction (hereafter “nesting activity”) can be readily monitored. Furthermore, reproductive success, defined here as the number of successfully emerged progeny, can be recorded from an individual cavity in which an individual bee has built a nest (Bosch and Vicens, 2006; CaraDonna et al., 2018; Wong and Forrest, 2021). *Megachile* (Latreille) is the most ecologically and morphologically diverse genus within the family (Gonzalez et al., 2019). *Megachile* spp., commonly known as leafcutter bees, use leaf pieces to construct nest cells. They have large chewing mandibles that can be used to cut out circular or oval pieces of leaf material; these leaf fragments are used to construct nest cells (Michener, 2007; Gonzalez et al., 2019). *Megachile* commonly nest above ground in pre-existing cavities in dried stems or trees (Danforth et al., 2019). Both *M. relativa* and *M. pugnata* are widespread across North America, prefer flowers for pollen and nectar in members of the

Asteraceae family, and nest readily in nesting-blocks (Medler, 1964; Tepedino and Frohlich, 1982; Forrest et al., 2019).

Experimental Design and Cavity Surveys

We set up a series of nesting-blocks prior to solitary bee activity in early spring (May) of 2012. Nesting-blocks were constructed from wooden blocks measuring 10 cm x 15 cm x 30 cm. To accommodate different sizes of solitary bees, each nesting-block had thirty cavities drilled of three different diameters (6, 7, and 8 mm). Each cavity was lined with a paper drinking straw to allow for easy removal of bee nests following emergence. Nesting-blocks were installed at 10 sites, each site approximately 100 m from the next nearest site. All sites were located within an approximately 2 km radius area and each had an approximate 100-150m diameter. At each site, 10 nesting-blocks were attached to the south facing part of live or dead trees on the south facing edges of meadows approximately 0.5 – 1.0 m above the soil surface. Each sites included montane wet and dry meadows, and aspen and spruce forests.

Each cavity in each nesting-block was checked with a pen light twice per week throughout the growing season (May–September) for nesting activity. Evidence of nesting activity included accumulated pollen, leaf fragments, mud, or the presence of actively nesting bees. The date on which we first observed any evidence of nesting activity in a given cavity was recorded as the nesting activity onset date. The date on which the cavities were plugged with mud or plant material (indicating nest completion) was recorded as the nesting activity end date. If the cavity was abandoned (clear evidence of activity, but not plugged) we determined the end date as the last day on which there was any activity observed. At the end of the growing season, cavities with nest activity were capped with a plastic vial to capture any emerging offspring the

following spring. After the first year of study, emergence of offspring in plastic vials was monitored concurrently with nesting activity throughout the season.

Female bees typically construct several nest cells within a single cavity. We considered the nest cells in a cavity to represent a single, nest-building event by an individual female bee; hence, our unit of replication is a cavity. Logistical constraints prevented us from marking and following the activity of individual bees. We acknowledge that female bees do not necessarily build only a single nest per block; indeed, one female can build multiple nests across cavities in a single nest block (Vázquez et al., 2023). Thus, it is possible that any individual female effects would be spread out across multiple cavities, and individual cavities within a nest block might not be totally independent from one another. It is more typical, however, that a single female nests in a single cavity (Jessica Forrest, *personal communication*). Thus, we do not anticipate the possibility of a single female nesting in multiple cavities affecting our results in a significant way.

Species identifications for each cavity were recorded if a female was observed building a nest during a survey and confirmed once offspring emerged in the following season. Otherwise, species identification for each cavity was solely determined once offspring emerged the following season. Other cavity-nesting bee species nested in our nesting blocks, but their abundance was either too low or they were not present in at least two years of the study, rendering them unable to address our research questions. The two species we focused on: (i) had at least 10 individual nests each year, and (ii) were present for at least two years of the study. All bees of a given species were considered a single population across all our study sites in a given year.

Quantification of nesting activity onset, duration, synchrony, and reproductive success

We quantified multiple dimensions of the phenological distribution of nesting activity: onset date, duration, and synchrony. We used nesting activity as a stand-in for reproductive activities (mating, egg laying), activities that are difficult to observe and quantify directly. We assumed that nesting activity followed mating, coincided with egg laying, and was followed by offspring development. However, we acknowledge that there may still be variation in the time period between these events and nesting activity. Nesting activity onset was defined as the nest start date (day of year) that was recorded for each cavity. The nesting activity duration (# of days) was calculated by subtracting the nest end date from the nest start date for each individual cavity. The synchrony of nesting activity was calculated following Augspurger (1983). Augspurger's Index of synchrony ranges between 0 and 1, with 1 indicating perfect synchrony. The index quantifies the overlap of nesting activity duration for each cavity relative to the rest of the population:

$$X^i = \left(\frac{1}{n-1}\right) \left(\frac{1}{f_i}\right) \sum_{j=1}^n e_{j \neq i}$$

X^i = The index of synchrony for an individual (i) within a population. $X = 1.0$ indicates perfect synchrony (i.e. all nesting days of an individual (i) overlap with all nesting days of all other individuals in the population.

n = the number of individuals in a population.

f_i = the number of days an individual (i) is nesting

e^j = the number of days both individuals i and j are nesting synchronously

We used the `aug_synchrony` function from the `AugspurgerIndex` package (Benkendorf, 2023) in R to calculate synchrony for this analysis.

Data Analysis

To evaluate interannual variation in nesting activity onset, duration, and synchrony, we compared the average annual onset, duration, and synchrony for individual cavities of each species across years. To compare these metrics, we used a one-way ANOVA with a Tukey post-hoc, or a Kruskal-Wallis with a Dunn post-hoc, for *M. relativa*, which was present in all three years of the study. We used t-tests for *M. pugnata*, which was present for two years of the study.

To understand the effect of nesting activity onset, duration, and synchrony on reproductive success, we regressed each metric for each cavity with the number of successful offspring produced by each cavity. Because our response variable, reproductive success, was measured as the count of emerged bees from an individual cavity, we used generalized linear mixed effects models with Poisson error distributions for each species. Each model included fixed effects of: (i) onset (day of year), (ii) duration (number of days), or (iii) synchrony (Augspurgers' Index). All models included year as a fixed effect to account for interannual variation in reproductive success that is unrelated to the fixed effects. In addition, each model included the identity of each nesting-block nested within the site as a random effect to account for variation between nesting-blocks and sites.

All analyses and plots were done in R (v4.2.0, R Core Team, 2022) with Tidyverse (v1.3.1, Wickham et al., 2019) and rstatix (v0.7.0, Kassambara, 2021). Mixed effects models were written with packages lme4 (v1.1-29, Bates et. al., 2015) and lmerTest (v3.1-3, Kuznetsova et. al., 2017), interpreted with car (v3.1-0, Fox & Weisberg, 2019), and models were checked for overdispersion and collinearity with the performance package (v0.9.0, Lüdtke et al., 2021).

Results

Across three years of study, we observed a total of 112 *Megachile relativa* nests from which 133 offspring survived to emerge as adults, and 43 *Megachile pugnata* nests from which 56 offspring survived to emerge as adults. Average nesting activity onset across all years was 17 July for *M. relativa* and 3 August for *M. pugnata* (Table 1). The average nesting duration across all years was 6.2 days for *M. relativa* and 7.2 days for *M. pugnata* (Table 1). Average nesting synchrony for individuals across all sites and years of the study was low overall: *M. relativa* had an average synchrony metric of 0.13 whereas *M. pugnata* had 0.18 (synchrony metrics range from 0-1, with 1 equaling perfect synchrony; Table 1).

We observed interannual variation in nesting onset and synchrony; in contrast, nesting duration was consistent across years for both species. We found that overall, onset of nesting activity varied across study years for each species (Figure 2 A & D). For *M. relativa*, average nesting onset date differed significantly across years ($X^2_2 = 17.5$, $p < 0.001$, Figure 2A); it was 12-15 days later in 2012 and 2013 compared to 2014 (Table 1). For *M. pugnata*, average nesting onset differed significantly between years ($t_{1,41} = 3.0$, $p = 0.002$, Figure 2D); like *M. relativa*, average nesting onset was 9 days later in 2012 compared to 2014 (Table 1; note that we did not observe any *M. pugnata* nesting in our nesting blocks in 2013). Duration of nesting activity was similar across study years for both species (*M. relativa*: $F_{1,2} = 0.33$, $p = 0.72$; *M. pugnata*: $t_{1,41} = 0.52$, $p = 0.61$, Figure 2B & E, Table 1). For *M. relativa*, synchrony of nesting activity differed significantly between years ($X^2_2 = 17.6$, $p < 0.001$, Figure 2C) with cavities in 2013 and 2014 having the higher average nesting activity synchrony, which was 0.5- 2.3x greater than 2012 (Table 1). For *M. pugnata*, synchrony of nesting activity also differed significantly between

years ($t_{1,19.8} = 2.8$, $p = 0.01$, Figure 2F), with cavities in 2012 having 1.5x greater synchrony than 2014 (Table 1).

The onset of nesting activity did not influence reproductive success for either species, but cavities with more synchronous nesting activity relative to the population were associated with higher reproductive success. Additionally, for one species, increased duration of nesting activity was positively associated with reproductive success. Nesting activity onset did not predict reproductive success for either *M. relativa* ($R_m^2 = 0.13$; Figure 3A, Table 2) or *M. pugnata* ($R_m^2 = 0.35$; Figure 3D, Table 2). There was no significant relationship between the duration of nesting activity and reproductive success for *M. relativa* ($R_m^2 = 0.14$; Figure 3B, Table 3), but there was a positive relationship between duration and reproductive success for *M. pugnata* ($R_m^2 = 0.55$; Figure 3E, Table 3). For both species, we observed a positive relationship between nesting activity synchrony and reproductive success (*M. relativa*: $R_m^2 = 0.15$; *M. pugnata*: $R_m^2 = 0.41$, Figure 3C & F, Table 4).

Discussion

Phenology is widely hypothesized to have important fitness consequences for organisms (Forrest and Miller-Rushing, 2010), but without considering the multiple dimensions of phenological distributions, we cannot fully understand how, why, and when phenological variation contributes to fitness outcomes (Ollerton and Lack, 1998). Our examination of the reproductive consequences of the nesting phenology of two closely related subalpine solitary bees over three years reveals that nest activity onset on its own did not predict reproductive success. Duration had different effects on the two bee species, and it was only synchrony that had a consistent effect on reproductive success across both species. Greater nesting synchrony had positive effects on reproductive success for both species. Our results indicate that without

considering multiple dimensions of nesting phenology—onset, duration, and synchrony—important reproductive consequences can be overlooked.

In contrast to the general hypothesis that variation in the onset of biological events will result in fitness consequences (e.g., Gross and Werner, 1983; Farzan and Yang, 2018), we do not find a relationship between nesting activity onset and reproductive success for either of our study species. This result is not caused by a lack of variability in onset. Indeed, we found strong interannual variability in nesting activity onset. Interannual variability in onset aligned with our expectations, especially considering the high interannual variability in climate conditions in our study area (Inouye et al., 2002; CaraDonna et al., 2014; Cordes et al., 2020; Ogilvie and CaraDonna, 2022). For example, early nesting activity start dates may benefit individuals through lower intraspecific competition, longer duration of reproductive periods (assuming end dates are fixed or vary less than onset dates), and predator avoidance (Iwasa and Levin, 1995; Straka et al., 2014). Furthermore, our results fall in contrast with recent research on other cavity-nesting bee species at our study site. Wong & Forrest (2021) found that cavity nesting bees with earlier reproductive timing exhibited longer reproductive periods and higher reproductive success; however, this work focused on early-season bees (*Osmia iridis*, *O. coloradensis*, *O. montana*, *O. subaustralis*, *Hoplitis fulgida*). Both our study species are members of the genus *Megachile*, which generally have much later activity periods than *Osmia* and *Hoplitis* such that earlier activity does not bring about a clear fitness benefit. The timing of events in early-season plants and animals tends to be more sensitive to changes in climate compared to their mid-season counterparts (Pau et al., 2011; Wolkovich et al., 2012; Chmura et al., 2019). The two focal species in this study are mid-season bees, and therefore may be less phenologically sensitive

relative to early-season counterparts. That is, there may be fewer advantages to begin nesting earlier.

We find evidence consistent with the hypothesis that longer durations of nesting activity result in reproductive benefits due to increased time for reproductive activity (Bosch and Vicens, 2006; Li et al., 2016; Wong and Forrest, 2021), however duration of activity did not vary between years. The consistency of nest activity duration between years may indicate a limitation in how quickly bees can complete a nest given foraging times and food availability between years. Longer durations of nesting activity were linked to increased reproductive success in *M. pugnata* but had no relationship with the reproductive success of *M. relativa*. The two species have similar ecological habits (nesting habits, floral resource use), so it is unlikely that their nesting activity or floral resource use account for the discrepancy in the relationship between nesting activity duration and reproductive success. Furthermore, the two species have similar nesting activity durations (Table 1), with *M. pugnata* nest building taking one more day on average than *M. relativa*. Although both bees are active in mid-season, *M. pugnata* starts nesting on average 1 – 2 weeks later than *M. relativa* (Table 1), when resources are likely still abundant, but may be dwindling compared to the time *M. relativa* is active. In addition, *M. pugnata* is 25% larger than *M. relativa*, which is the smallest Megachile in the subalpine ecosystem (Pardee et al., 2022). It is reasonable to expect that larger bees require larger larval provisions, and increased nest activity duration would ensure that *M. pugnata* bees obtain the necessary provisions for development.

Although investigated much less than onset and duration, within-population synchrony is also hypothesized to be an important dimension of phenological distributions that can have reproductive consequences (Augspurger, 1983; Ims, 1990a; Elzinga et al., 2007). Our results are

consistent with this hypothesis. We found a positive relationship between synchrony of nesting activity and reproductive success for both species, as detected previously in plants (Augspurger, 1983; Ims, 1990a; Elzinga et al., 2007; Waananen et al., 2018). In addition to variation in average synchrony across years. This positive effect of increased synchrony on reproductive success has various potential explanations, including synchronization with favorable climate conditions and critical resources, increased mating opportunities, and predator swamping (the inundation of prey that overwhelms a predator population) (Ims, 1990a; Ims, 1990b). Our focal species are actively nest-building for only a few weeks during the middle of the growing season, when temperatures do not vary substantially. Therefore, these bees are unlikely to be constrained by climate conditions. In addition, their preferred floral resources, species in the Asteraceae, are abundant throughout the growing season for these two species (Tepedino and Frohlich, 1982; Strickler et al., 1996; CaraDonna et al., 2014; CaraDonna et al., 2017; CaraDonna and Waser, 2020).

Another potential explanation for the positive relationship between synchrony and reproduction is more synchronous individuals having greater access to mates. In this system, greater access to mates can result from protandrous emergence, which is common for solitary nesting bees (Eickwort and Ginsberg, 1980; Danforth et al., 2019). It is reasonable to assume that the sooner females can mate, the sooner they can start building nests and produce offspring. When the population is at its highest nesting synchrony, this likely coincides with high availability of mates shortly after females emerge. Finally, antagonists can be a strong selective force in cavity-nesting bee population regulation, including in our study location (Forrest and Chisholm, 2017).

Concentrated nesting will attract predators, not only mates (Weislo, 1996). Thus, it is plausible that individuals with higher individual synchrony experience predator swamping (Ims, 1990b), ultimately increasing average reproductive success among individuals. Although we cannot